

The United Equation of Animal Growth

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Abstract: The equation that can describe all known types of animal growth is proposed. The equation contains two basic coefficients, one of which determines the initial rate of growth; the other determines the change of the growth rate. In separate cases two correction coefficients should be taken into account, one of which is connected with morphogenetic processes and the other is connected with spontaneous decrease of the body weight. Biorhythms that accompany growth process can be described by the equation as well. Linear recursive form of the equation allows to use regression analysis and, therefore, comparative intrapopulation, interpopulation and interspecies analysis of growth. Examples of approximation by the equation of own and literature experimental data are shown. Values of the coefficients of the equation for different types of growth in different stages of ontogenesis of the various animal systematic groups are calculated. The equation is suitable to describe change of any biological parameter which is associated with body weight by allometric (power) dependence.

Keywords: Body Weight Changes, Developmental Biology, Growth, Mathematical Model

1. Introduction

Growth is one of the main processes occurring during animal development. Therefore, it is not surprising that its description is a subject of many studies [1-9].

All the observed growth curves can be divided into two broad categories [10,11].

1. Infinite growth. The size of the animal is permanently increased. Such growth is observed in the majority of poikilothermic animals.

2. Finite growth. The size of the animal first reach maximum and then continuously decrease. Such growth is characteristic for some poikilothermic and for most homoeothermic animals.

Each of these categories can be divided by several types depending on the shape of growth curve: exponential, parabolic, linear, decelerating and S-shaped. It should be noted that the types of curves are not limited by the above types. Cases of absence of weight change or even degradation of body weight are often observed for some ontogenetic periods. Usually, these changes are not considered as growth [3,4]. I believe that such point of view is not entirely true, because result of growth depends on the balance between processes of assimilation and dissimilation. Thus, cases of weight decreasing can be considered as "negative" growth

when dissimilation prevails over the assimilation. The problem of quantitative description of the growth is complicated by the fact that, as a rule, is accompanied by biorhythms, having both exogenous and endogenous nature [12,13].

At first view, it is impossible to find a single equation that can describe all observed types of growth. Large number of equations was proposed, which more or less well describe different growth curves [14]. However, a single equation that can describe all of the observed growth curves still has not been found.

Nevertheless, detailed analysis of the dependence of the body weight or length (M) on age (t) indicated that at least for the infinite growth only three basic equation can be used [2].

1. The exponential equation:

$$M = B(1 + Ae^{k_g t})^{1/b} \quad (1)$$

All the coefficients of this equation are positive.

2. Parabolic equation:

$$M = B(1 + At^{k_g})^{1/b} \quad (2)$$

An important special case of (2) is a linear equation when the coefficients k_g and b equal 1.

3. The asymptotic equation. This equation is called the von

Bertalanffy growth equation and is used most often:

$$M = M_{\infty} (1 - Ae^{k_g t})^{1/b}; \quad (3)$$

$k_g < 0$; all other coefficients are positive. If $0 < b \leq 1$, then (3) describes the asymptotic decelerating growth type (convex curve without inflection). If $b > 1$, (3) describes the asymptotic S-shaped growth type with one point of inflection. To calculate the values of the coefficients of (3) one often uses recurrent form of this equation [15,16]:

$$M_{t+m}^b = cM_t^b + d \quad (4)$$

M_t is growth parameter at the age t ; M_{t+m} is growth parameter at the age $t + m$; b is constant from Bertalanffy equation (3); m is the time interval between measurements.

It appears that all these equations can be reduced to one, which describes not only an infinite growth, but all types of observed growth curves. Deduction and analysis of such united equation is an aim of this article.

2. Methods

The equations (1)-(4) were used as a basis for deduction of united growth equation. The possibility of the united growth equation to fit experimental data was tested on own and literature experimental data. Coefficients of the united equation were determined by methods of regression analysis. The suitability of the equation is evaluated by the criterion of nonlinearity [17].

Fitting of data by united equation and the construction of the time series were performed by program Matlab (version 7.3.0.267, developed by The MathWorks, Inc, USA). To distinguish main trend and rhythmic processes from the time series singular spectrum analysis were used (program "Caterpillar", version 3.40, developed by GistaT Group, Russia). Following options in program "Caterpillar" were: the window length is half of the number of data; without centering [13].

3. Results and Discussion

First of all, we note that all of the growth equations (1)-(4) contains a power coefficient b . The value of this coefficient depends to a large extent on whether the parameter has been measured. Shmalgauzen [1] proposed to use cube root of the mass as a parameter of "pure" growth. I propose to use this term for the parameter $Z = M^b$. Then (1)-(3) have the simplest

forms: $Z = \frac{V_0}{\ln c} (c^t - 1) + Z_0$ for (1) and (3) and

$Z = V_0 t + Z_0$ for (2); Z_0, V_0 are initial values of Z and its rate respectively, when $t = 0$; c determines the change of V_0 with age. Both these equations can be written in the joint differential form:

$$\frac{dZ}{dt} = \frac{dM^b}{dt} = V_0 c^t. \quad (5)$$

Evaluation of the coefficients of (5) can be carried out using the recurrence formula similar to the Ford-Walford equation (4), which is usually used for estimation of Bertalanffy equation coefficients:

$$Z_{t+m} = c^m Z_t + d; \quad (6)$$

V_0 from (5) is calculated as $V_0 = (Z_0 - d) \ln(c)$, if $c > 0$ and $c \neq 1$; $V_0 = d/m$, if $c = 1$.

The plot of (6) in the coordinates $Z_{t+m}(Z_t)$ is a vector whose start point has coordinates $(Z_1; Z_{m+1})$ and end point has coordinates $(Z_{t-m}; Z_t)$, where Z_1, Z_{m+1} are the first and the second measurements; Z_{t-m}, Z_t are the penultimate and the last measurements respectively. Type of growth curve is determined by the position on the plot and the degree of slope of the vector (Fig. 1).

The values of the coefficients of (6) for infinite growth of the species of different taxa at different developmental stages are given in Table 1. Since the value of coefficient c depends on the units of age, and the value of coefficient d depends on the units of growth parameters, Tables 1 and 2 contain corresponding units used by authors of data. Fig. 2a-e shows the examples of approximation of infinite growth by (5).

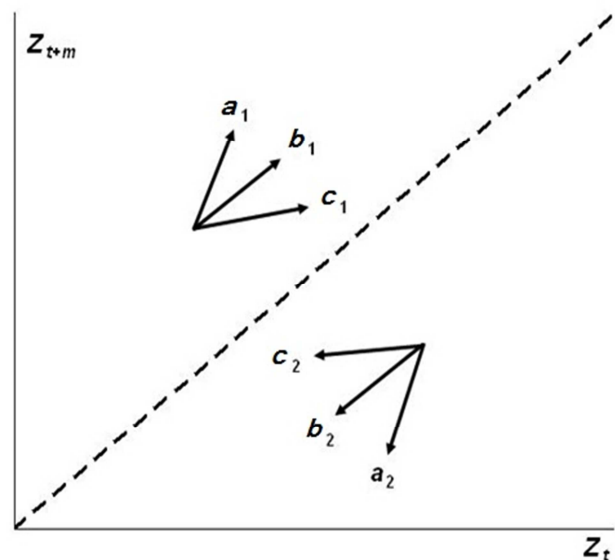


Figure 1. Plots for (2). Dashed line is the bisector of the coordinate axes. Indexes: 1 - the increase of parameter Z ; initial coordinates of the vectors lie above the bisector; 2 - the decrease of parameter Z ; initial coordinates of the vectors lie below the bisector. Types of growth: a – an exponential ($c > 1$); b – a linear ($c = 1$); c – an asymptotic decelerating ($c < 1$).

Situation is more complicated in the case of finite growth. I believe that weight reduction occurring in this case after reaching a maximum determined by the spontaneous decay of the body, the rate of which is proportional to the body weight [39]. Therefore, I introduced corresponding amendment in the calculation of the "pure" growth parameter:

$$Z = (Me^{vt})^b; \quad (7)$$

v is the rate of spontaneous decay of the body. If $v = 0$ then we return to previous version of (5).

Table 1. Coefficients of (6) for infinite growth.

Species	Stage	c	d	Data source
Exponential growth type ($c > 1$)				
<i>Bacillus megatherium</i>	Cell cycle	1.011±0.001 (min)	15±42 (nm)	[1]
<i>Planorbarius corneus</i>	Larvae	1.037±0.006 (h)	-12.1±6.5 (µm)	[18]
<i>Leptestheria dahalacensis</i>	Larvae	1.050±0.015 (d)	0.72±0.23 (µg)	[19]
<i>Pleurodeles waltl</i>	Larvae	1.028±0.001 (d)	-0.38±0.41 (mm)	[20]
Parabolic (linear) growth type ($c \approx 1$)				
<i>Planorbarius corneus</i>	Embryos	0.996±0.003 (h)	55±12 (µm)	[18]
<i>Octopus bimaculoides</i>	Adults	1.001±0.001 (d)	0.30±0.06 (g)	[21]
<i>Chirocephalus iaphanus</i>	Adults	0.999±0.036 (d)	0.99±0.15 (mm)	[22]
<i>Heterozius rotundifrons</i>	Embryos	1.005±0.054 (d)	0.41±0.28 (mg)	[23]
<i>Mamestra brassicae</i>	Caterpillar	0.997±0.023 (d)	0.28±0.13 (mg)	[24]
<i>Ambystoma mexicanum</i>	Embryous	0.998±0.002 (h)	1.41±0.25 (mm)	[25]
<i>Lacerta agilis</i>	Adults	1.00±0.02 (months)	0.39±0.03 (g)	[26]
<i>Gallus gallus</i>	Embryos	1.01±0.02 (d)	0.15±0.02 (g)	[27]
Asymptotic decelerating (S-shaped) growth type ($c < 1$)				
<i>Micrococcus sp.</i>	Cell cycle	0.975±0.099 (min)	265±5 (nm)	[1]
<i>Lymnaea stagnalis</i>	Adults	0.884±0.005 (weeks)	4.41±0.16 (mg)	[28]
<i>Planorbarius corneus</i>	Adults	0.937±0.014 (weeks)	0.60±0.12 (mg)	[18]
<i>Margaritifera laevis</i>	Adults	0.922±0.013 (years)	0.83±0.09 (g)	[29]
<i>M. margaritifera</i>	Adults	0.927±0.002 (years)	0.35±0.01 (mm)	[12]
<i>Mytilus edulis</i>	Adults	0.942±0.017 (years)	7.61±0.67 (g)	[30]
<i>Daphnia magna</i>	Adults	0.891±0.011 (d)	324±44 (µm)	[31]
<i>Inahus dorsettensis</i>	Larvae	0.959±0.063 (d)	11.02±5.38 (mg)	[32]
<i>Leptinotarsa decemlineata</i>	Larvae	0.970±0.021 (d)	0.33±0.09 (mg)	[33]
<i>L. decemlineata</i>	Imago	0.753±0.040 (d)	3.46±0.24 (mg)	[33]
<i>Blatella germanica</i>	Imago	0.895±0.003 (d)	0.55±0.07 (mg)	[34]
<i>Apostichopus japonicus</i>	Adults	0.727±0.002 (years)	2.00±0.01 (g)	[35]
<i>Clupea harengus</i>	Adults	0.748±0.003 (weeks)	1.94±0.03 (g)	[36]
<i>Pleurodeles waltl</i>	Larvae	0.992±0.002 (d)	0.14±0.02 (g)	[37]
<i>P. waltl</i>	Adults	0.960±0.001 (weeks)	0.10±0.01 (g)	[18]
<i>Lacerta agilis</i>	Embryos	0.986±0.069 (d)	1.07±0.41 (mg)	[26]
<i>Homo sapiens</i>	Embryos	0.988±0.004 (weeks)	0.52±0.04 (g)	[38]

Note: The average values of the coefficients and standard error of the mean are shown; dimensions of the age and growth parameters are shown in parentheses; n is number of measurements.

Table 2. Coefficients of (6) for finite growth.

Species	c	d	v	Data Source
Exponential growth type ($c > 1$)				
<i>Ambystoma mexicanum</i>	1.051±0.005 (months)	0.18±0.06 (g)	0.105±0.002	[40]
Parabolic (linear) growth type ($c \approx 1$)				
<i>Deroceras reticulatum</i>	0.996±0.019 (weeks)	0.95±0.35 (mg)	0.040±0.001	[41]
<i>Acheta domesticus</i>	1.002±0.001 (d)	0.37±0.06 (mg)	0.0079±0.0001	[42]
<i>Homo sapiens</i>	0.995±0.001 (months)	0.59±0.03 (kg)	0.0003±0.0001	[43]
Asymptotic decelerating (S-shaped) growth type ($c < 1$)				
<i>Enchytraeus albidus</i>	0.925±0.008 (d)	0.36±0.06 (g)	0.0003±0.0001	[44]
<i>Deroceras agreste</i>	0.883±0.037 (weeks)	1.17±0.30 (mg)	0.017±0.008	[45]
<i>Rattus norvegicus</i>	0.687±0.015 (months)	4.68±0.09 (g)	0.0020±0.0002	[46]
<i>Coturnix coturnix</i>	0.956±0.002 (d)	1.48±0.03 (g)	0.0011±0.0002	[47]
<i>Tyto alba</i>	0.945±0.006 (d)	1.15±0.10 (g)	0.0013±0.0004	[48]

Notes: The average values of the coefficients and standard error of the mean are shown; dimensions of the age and growth parameters are shown in parentheses; v is correction factor from (7). The data obtained for adults in all cases, besides *A. mexicanum* for which larvae (axolotl) was measured.

Values of the coefficients of (5) for finite growth of the species from different taxa at different developmental stages are shown in Table 2.

Fig. 2f shows an example of finite growth description by (5).

Some special cases have separate interest. Thus, if $V_0 = 0$ or $c = 0$, the parameter Z is kept constant, i.e. the size of the body does not change. The plot of the function $Z_{t+m}(Z_t)$ is represented by a point with coordinates $(Z_0; Z_0)$.

If $V_0 < 0$, the parameter of growth decreases. The plot of the function $Z_{t+m}(Z_t)$ is the vector lying below the bisector (Fig. 1).

Thus, (5) and (6) can describe age related degradation of the weight. For example, weight loss during pupal stage of beetles *Leptinotarsa decemlineata* [33] is described by these equations with coefficients $c = 0.981 \pm 0.046$; $d = 0.07 \pm 0.224$; $V_0 = -4.16 \pm 5.24$ (number of measurements $n = 18$) (Fig. 3). For pupae of butterflies *Bombix mori* [47] $c = 0.934 \pm 0.023$; $d = 1.30 \pm 0.34$; $V_0 = -0.71 \pm 0.46$ ($n = 20$); for adults *B. mori* [47]

$c = 0.949 \pm 0.030$; $d = 0.55 \pm 0.19$; $V_0 = -4.16 \pm 5.24$ ($n = 11$); for adults *Mamestra brassicae* [24] $c = 0.936 \pm 0.052$; $d = 0.85 \pm 0.76$; $V_0 = -0.048 \pm 0.007$ ($n = 9$); during cleavage stage of snails *Planorbarius corneus* (own data) $c = 1$; $d = 5.3 \pm 2.6$; $V_0 = -2.80 \pm 0.13$ ($n = 215$). In all examples the age is measured in days from the larvae hatching, body weight is measured in mg, except the embryos of *P. corneus* for which age is measured in hours from first division, length is measured in μm .

The case with a negative coefficient c has separate interest. Such differential equations include wave components [49-51]

associated with the appearance of an imaginary part in the value of the power factor $k_g = \ln(c)$ from (1)-(3).

Endogenous biorhythms of specific growth rate have been identified and described for some species of gastropods and bivalves [12,13]. Such biorhythms are believed to be characteristic for the growth of a variety of animal taxa [12]. Accounting of biorhythms allows more fully describe the process of growth. An example of such a description is shown in Fig. 3.

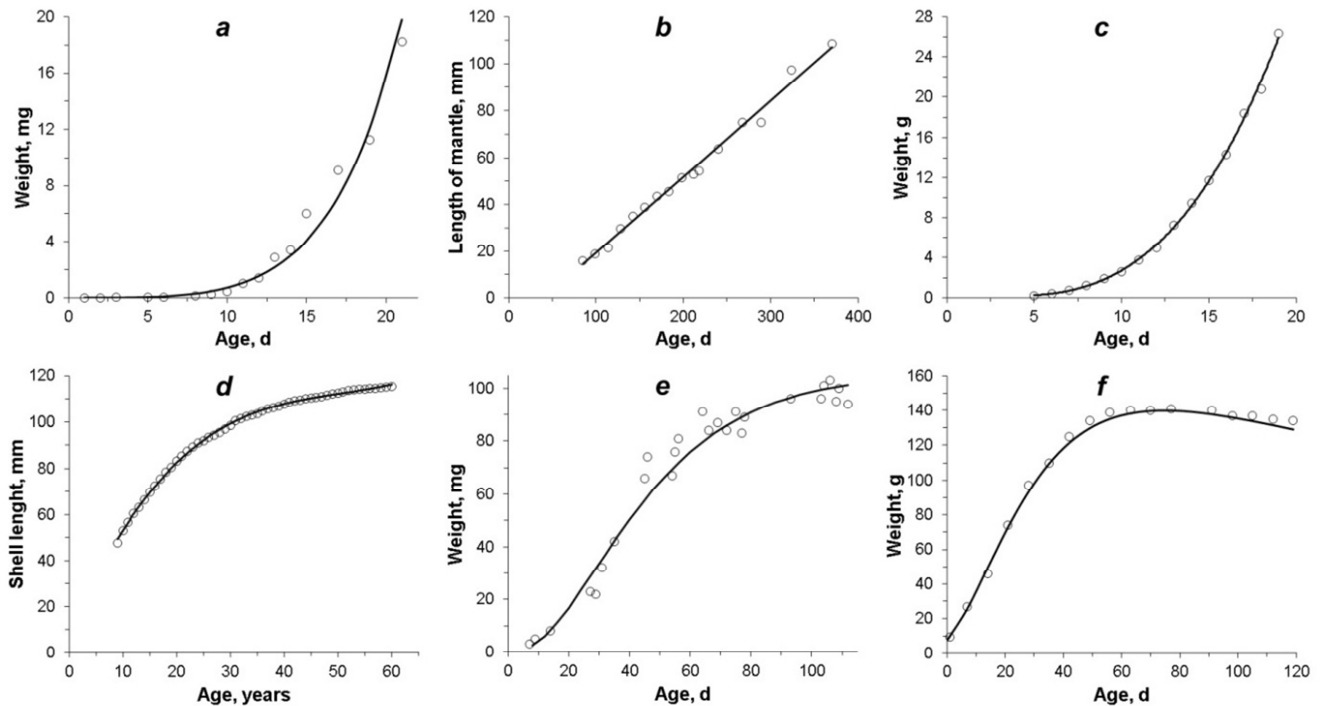


Figure 2. Examples of growth curves and their approximation with united equation (5). Circles are experimental data. Curves are plots of the function (5). a - an exponential growth type; *Leptostheria dahalacensis* (Branchiopoda), larvae and juvenils [19]; b - a linear growth type; *Octopus bimaculoides* (Cephalopoda), adults [21]; c - parabolic growth type; *Gallus gallus* (Aves), embryos [27]; d - asymptotic decelerating growth type; *Margaritifera margaritifera* (Bivalvia), adults [12]; e - asymptotic S-shaped growth type; *Blatella germanica* (Insecta), adults [34]; f - finite S-shaped growth type; *Coturnix coturnix* (Aves); adults [47].

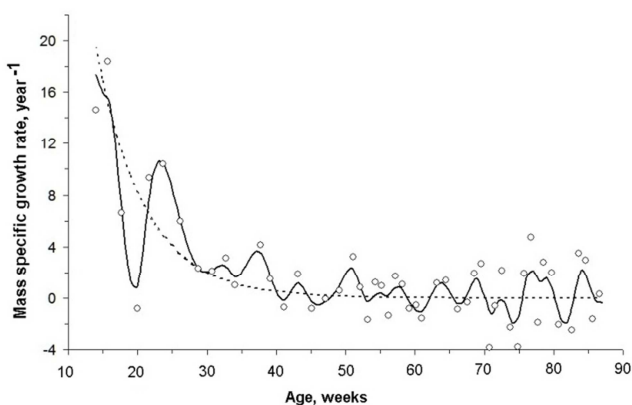


Figure 3. The plot of the specific growth rate versus the age for *Lymnaea stagnalis* (Gastropoda) [13]. Circles are experimental data. The dashed curve is the main trend describing by (5) with a positive coefficient c . The solid curve is the sum of the main trend and wave components, determined by the case of negative coefficient c .

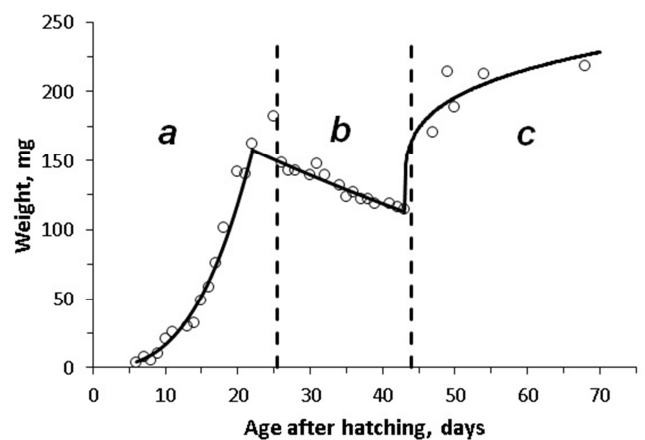


Figure 4. Weight change during different developmental stages of the beetles *Leptinotarsa decemlineata*. Circles are experimental data [33]. Vertical dashed lines are the borders of developmental stages: a - the larvae; b - the pupa; c - the imagoes. Solid line shows different growth curves in different developmental stages, approximated by (5) with different coefficients.

The equation (5) can be called the united growth equation, since it describes any type of animal growth observed in the nature. Type of growth is determined mainly by the value of the coefficient c : if $c > 1$, the dependence of $Z(t)$ is exponential; if $c = 1$, the dependence is linear; if $0 < c < 1$ the dependence is asymptotic.

The existence of an equation capable to describe all known growth types indicates that for prolonged developmental stages the growth process seems to be in accordance with the physical and the chemical laws. Final result depends on the balance of the rates of assimilation, dissimulation and spontaneous disintegration of the biological system [1,3,4]. This does not mean that equation coefficients remain unchanged throughout the lifespan. Growth is too important process to leave it without control and regulation [8,9,52]. It is most likely that the regulation occurs over relatively small period of time by changing the rates of biosynthesis and reactions leading to disintegration of biomolecules. Hereafter, the process goes spontaneously until the moment when necessity of further regulation occurs. Such necessity may be connected with the achievement of a certain stage of development, the influence of external factors and/or the changes in physiological state.

Changing of growth type from stage to stage occurs in the majority of species. Thus, the birds' embryos grow by parabolic type (Fig. 2c), whereas after hatching S-shaped finite growth type occurs (Fig. 2f).

Our data show that during embryogenesis of snails *Planorbarius corneus* stages with different types of linear growth sequentially replaced: decreasing of sizes (cleavage), constant sizes (blastula and gastrula), exponential growth (larvae stages), asymptotic or linear types of growth (postlarval stages) [18].

The sharpest change in the type of growth is observed during development of insects with complete metamorphosis (Fig. 4). Increase of larvae weight is replaced by weight degradation during the pupae stage. Weight of adults can increase [33] or decrease [24,47] due to species.

Nevertheless, at each developmental stage (5) is quite suitable to describe animal growth. Only the values of the coefficients are changed.

Power (allometric) dependence is often occurred between growth and a number of other biological parameters [4,53]:

$$Y = aX^b; \quad (8)$$

Y , X are measured parameters; a , b are coefficients.

Therefore, the equation (5) is suitable to describe any type of animal growth, as well as change of any biological parameter which is associated with body weight by allometric (power) dependence (8). For example, linear or weight sizes of organs, rate of metabolism etc. [53,54].

4. Conclusion

Proposed equation is very simple. It contains only two main coefficients and two additional coefficients for special cases of growth. Coefficients of (5) have quite clear biological

interpretation. V_0 determines the initial rate of the growth; c determines the character of growth rate change; b defines the impact of morphogenetic processes into growth process; v determines the rate of spontaneous decay of the body.

A small number of coefficients allow easily approximate the experimental data by (5). Presence of a linear form (6) allows comparative intrapopulation, interpopulation and interspecies analysis of the growth.

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